Title: Hunter-gatherer multilevel sociality accelerates cumulative cultural evolution

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One Sentence Summary: Hunter-gatherers from different bands form fluid social networks that facilitate cultural innovation through recombination of cultural traditions.

Abstract:

Although multilevel sociality is a universal feature of human social organisation, its functional significance remains unclear. Here, we investigated the effect of multilevel sociality on cumulative cultural evolution by using wireless sensing technology to map inter- and intra-band social networks among Agta hunter-gatherers. By simulating the accumulation of cultural innovations over the real Agta multi-camp networks, we demonstrate that multilevel sociality accelerates cultural differentiation and cumulative cultural evolution. Our results suggest that hunter-gatherer social structures based on (i) clustering of families within camps, and camps within regions; (ii) cultural transmission within kinship networks, and (iii) high inter-camp mobility may have allowed past and present hunter-gatherers to maintain cumulative cultural adaptation despite low population density, a feature that may have been critical in facilitating the global expansion of *Homo sapiens*.

Main Text:

Multilevel sociality and a unique ability to accumulate culture are key human adaptations, and evolved in ancestral humans who adopted a hunter-gatherer lifestyle. Hunter-gatherer multilevel sociality is defined by a uniquely fluid social structure, nuclear family units, high between-camp mobility, and multi-locality (*1*-*5*). Genomic studies (*6*) have shown that fluid social structures already characterised expanding Upper Palaeolithic human populations. Meanwhile, long-range cultural exchange in the *Homo sapiens* lineage date back to at least 320kya (*7*). The emergence of both multilevel sociality and advanced cumulative culture early in the human lineage suggests an evolutionary link between the two processes. To investigate the effect of multilevel sociality on the dynamics of cultural evolution in humans, we (i) mapped inter- and intra-band social networks of Agta hunter-gatherers; (ii) designed agent-based simulations to model the virtual creation of a complex medicinal drug across the real Agta social network; and (iii) compared results of these simulations to similar simulations run across social structures lacking the unique features of hunter-gatherer multilevel sociality.

First, we mapped interactions among all adults in two multi-camp Agta communities in the Philippines (7 forest camps over 36 km^2, 54 adults, 29 females; and 3 coastal camps over 5 km of coast and 25 km^2, 37 adults, 17 females; Fig. 1). We used wireless sensing technology (*3*) to record all dyadic interactions within 3 meters, every 2 minutes, over a month. The weight of a dyadic link was defined as the number of times the dyad was recorded during the month. Data show that camps are connected by frequent migrations and visits, reflecting the reported high mobility of hunter-gatherers (*8*, *9*). In the forest multi-camp experiment, 41% (593 of 1431) of all possible inter- and intra-camp dyads were recorded at least once (unweighted dyads), against 86% (583 of 666) in the coastal group. Intra- and inter-camp networks varied in density. In the forest group, 66.2% (219 of 331) of possible intra-camp dyads were recorded, against 34% of inter-camp dyads (374 of 1100). In the coastal group, 84% (294 of 349) of the possible intra-camp dyads were observed, against 91% of possible inter-camp dyads (289 of 317). However, when weights are considered, intra-camp dyads are more strongly connected in both groups. For example, only 36.9% of unweighted forest dyads were intra-camp, while 49% (10354 of 21048) of weighted dyads were intra-camp. In the coastal group, 54.1% of unweighted dyads were intra-camp, against 73.6% (23483 of 31901) of weighted dyads. In summary, coastal camps are denser

and more interconnected than forest camps, and intra-camp dyads are stronger than inter-camp dyads in both groups.

Relatedness level is also a factor, as most dyadic relations (both unweighted and weighted) are among non-kin (Table S1), reflecting hunter-gatherer's co-residence mostly with unrelated individuals (*1*). Non-kin dyads play an important role in binding the multi-camp structure together, as the proportion of non-kin dyads is higher among inter-camp than among intra-camp interactions. Finally, we found no sex biases in unweighted dyads in either coastal or forest groups (at both intra- and inter-camp level), reflecting the sex-egalitarianism of hunter-gatherer societies (*1*; Table S2). When dyadic weights are considered, no consistent sex bias is found either, with an over-representation of male-male intra-camp dyads at the expense of female-female dyads in the forest camp, but the opposite pattern on the coast. Together, the results show a hierarchically structured multi-camp social network, with households mostly consisting of close kin, but dyads between households and between camps consisting mostly of non-kin, with few observed differences between men and women (*3*).

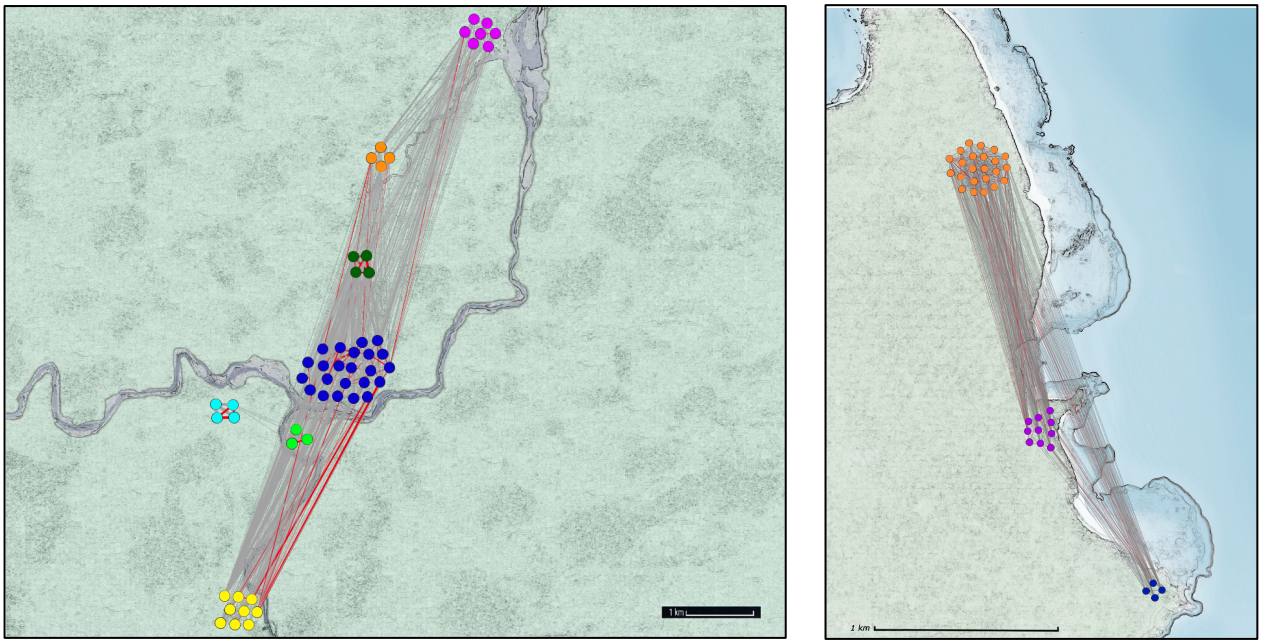

Fig. 1. **Multi-camp structures in Agta hunter-gatherers.** Figure displays individuals (dots) in camps (dot colours). Width of lines connecting individuals is proportional to dyadic weights (non-kin links: grey lines; close kin links: red lines). A) Forest camps, B) Coastal camps. Scale bars: 1 km. Locations of camps (7 forest, 3 costal) and camp sizes are approximate.

Next we tested the potential effect of hierarchical multi-camp network structure on cumulative cultural evolution. We adapted a computer-based experiment (*10*) to compare cultural evolution rates under distinct social network structures. We first ran the experiment as a simulation across the real Agta multi-camp networks. In the simulations, agents had to discover successive innovations by combining virtual medicinal plants, replicating actual processes observed in hunter-gatherer populations (*11*). Agents were originally given six medicinal plants, each deriving a drug with a medicinal value. In each round, two agents formed a dyad and combined three of their medicinal drugs, without repetition and selected in proportion to their medicinal value. The medicinal value of the resulting triad was calculated from the value of the three

components (Fig. 2; details in Supplementary File). Of the possible 20 initial triads, we established that only one led to the creation of a superior phytomedicine A1, and another one to phytomedicine B1. Those two new, higher-order innovations became new ingredients added to the original set. A1 could be combined again in one unique drug triad to produce the superior phytomedicine A2, which in its turn was necessary in a triad producing A3. The same happened in the parallel trajectory of increasing medicinal value from B1 to B2 and B3. At the fourth and highest level of innovation in the simulation, a 'crossover' or recombination of the two trajectories was necessary to produce the two phytomedicines with highest efficiency (crossover 1, which derived from the triad A2, A3 and B3; or crossover 2, which required B2, B3 and A3). The virtual experiment was finished when either crossover 1 or 2 was discovered by two agents. This design aimed to reflect key components of cultural evolution ('ratchet effect', incremental improvement, recombination and innovation; *12*). To implement the simulation across real hunter-gatherer networks, in each round *t* an agent *i* was selected randomly, and its partner *j* was selected with a probability proportional to the weights of all dyadic interactions of *i* in the real hunter-gatherer network. When a new ingredient was discovered, it was automatically transmitted to all direct network neighbours of both *i* and *j*.

We ran 1000 simulations across the real multi-camp networks of forest and coastal groups. The forest group required on average 230.5 (±313) trial rounds to discover the crossover drug, and the coastal group 646.7 (±572) rounds (Fig. 3A, Table S3). Next we ran the same experiment over size-matching fully connected networks, where all individuals are network neighbours and hence any innovation is immediately transmitted to all network members. Crossovers took significantly more rounds both in the forest group (477.3±413; Wilcoxon rank test, $W=242750$, $P<0.001$) and coastal group (697.7±569.2; Wilcoxon rank test, $W=464790$, $P=0.006$), although for the coastal group the absolute difference between the two conditions was less pronounced, possibly due to the coastal group being more densely connected and hence more similar to its size-matching fully connected network. Therefore, the sparsely inter-connected social structure of hunter-gatherer multi-camps accelerates cultural evolution.

Ethnographic studies have shown that hunter-gatherer medicinal plant knowledge is preferentially transmitted through kin networks rather than freely available to all network neighbours (*11*). Therefore, we repeated our experiment in real networks but limited transmission of new discoveries to close kin neighbours in the network (father, mother, offspring, siblings and spouses). The result is further acceleration of innovation rates in comparison to transmission to all direct neighbours in size-matched fully connected networks, with crossovers now taking only 51.1 (±77.1) rounds in the forest group (Wilcoxon rank test, $W=225460$, $P<0.001$) and 119.8 (±293.7) in the coastal group (Wilcoxon rank test, $W=82181$, $P<0.00001$) (Fig. 3A).

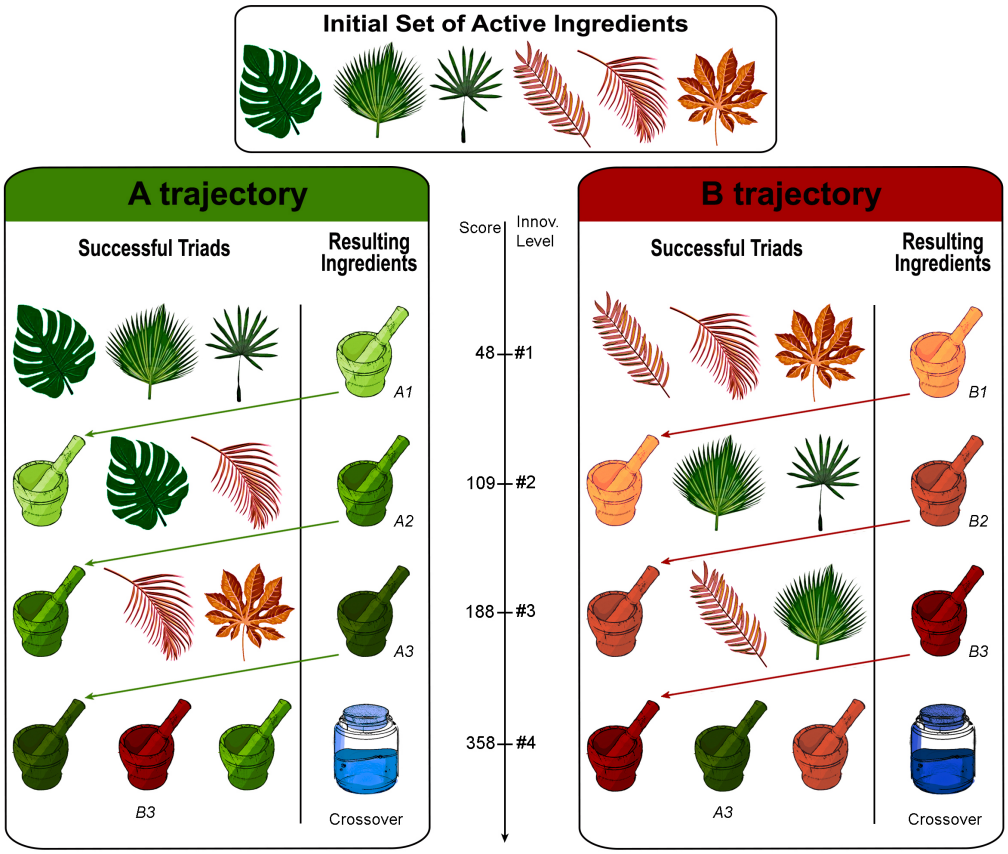

Fig. 2. Cumulative culture simulation. In our simulation, agents had to discover successive innovations by combining virtual medicinal plants. They were given an initial set of six medicinal plants, which could be combined in triads to generate new drugs (A1/A2/A3, B1/B2/B3) of increasing medicinal value. At the fourth level of innovation, a 'crossover' of trajectories A and B produces the two medicines with highest efficiency (crossovers 1 and 2). The virtual experiment was finished when a crossover was discovered. Figure and simulation adapted from (*10*).

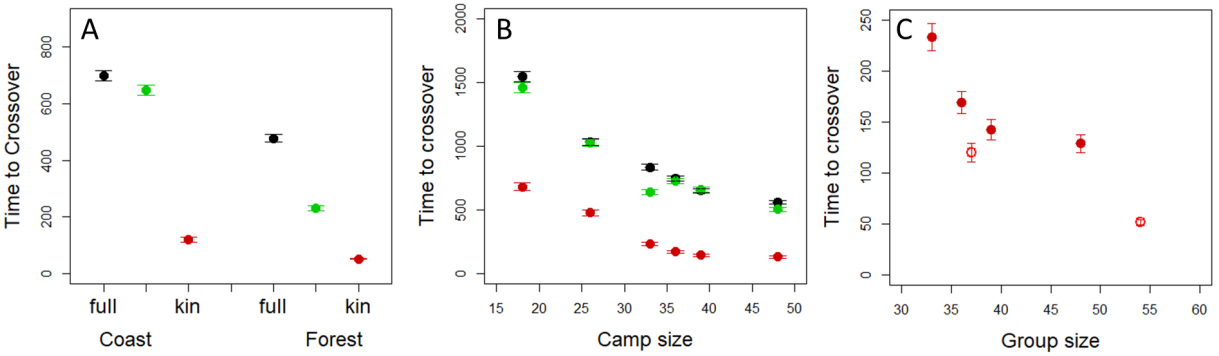

Fig. 3. Time to discovery of highest-level innovation (crossover). A) Time to crossover in multi-camp simulations (coast and forest) under three experimental treatments (black: fully connected; green: all neighbours copy; red: only close kin copy). B) Time to crossover in six individual camps. C) Comparisons between individual camps (red circles) and real multi-camps of similar size (open circles), indicating independent effects of network size and structure.

A recent study (*3*) has provided evidence that structural network properties of hunter-gatherer residential camps (global efficiency, clustering) maximise the efficiency of information transmission within camps. Such properties result from households mostly consisting of close kin, and households being interconnected through strong but more sparse non-kin dyads. We therefore replicated simulations as above, but here only considering intra-camp interactions under three scenarios: fully connected networks, real hunter-gatherer networks with transmission to all neighbours, and real hunter-gatherer networks but limiting transmission to close kin only. We first used network data from six separate Agta camps, previously described in (*3*). In simulations across fully connected networks, time to produce the final medicine ranged from 557.9 to 1545.3 rounds depending on the size of the camp (Fig. 3B). In real networks with transmission of innovations to all neighbours, time to crossover remains broadly similar (from 503.3 to 1460 rounds), with no significant differences between the two conditions in four of the six camps (Table S3). In contrast, when transmission of discoveries is limited to close kin neighbours, we observe a significant acceleration in innovation rate, with average time to crossover reduced to between 128.7 and 680.8 rounds. For all six camps, transmission of innovations only to close kin halves time to crossover in comparison to transmission to all neighbours. There is also a positive effect of camp size (Fig. 3B), confirming the importance of demography in cultural evolution (*13-17)*. However, effects of social structure and size are independent (*18*, *19*). This is demonstrated by our simulations across the two multi-camp groups, which resulted in shorter times to crossover than in the case of single camps of approximately similar size (Fig. 3C). For example, in the coastal multi-camp group (n=37) with transmission to close kin only, mean time to crossover was 119.8 rounds, significantly shorter than for single camps with equivalent population size, such as camp 4 (n=36; 169 rounds, Wilcoxon rank test, W=424970, P<10-8) and camp 6 (n=39; 142.5 rounds, Wilcoxon rank test, W=458470, P=0.0013) (Fig. 3C, Table S3). Thus, while intra-camp social structure facilitates the evolution of cumulative culture due to kin clustering, sparsely connected multi-camp social structures further accelerate cultural innovation rates.

We then asked how and why a multilevel social structure that restricts the flow of information can increase rates of cultural evolution. We thus analysed the distribution of incremental

innovations (A1, A2, A3, B1, B2, B3) and recombination events (crossovers) across the social network at the end of simulations. Simulations based on transmission of innovations only to close kin revealed that the structuring of the two multi-camp networks (with families within camps, and camps within a multi-camp) promotes cultural clustering, overall diversity, and faster times to crossover, compared to transmission to all nodes in fully connected networks (Fig. 4). The reason is that fully connected networks promote faster transmission of innovations to all network members along one of the lineages A or B. However, faster discoveries of incremental innovations along one trajectory happens at the expense of discoveries in the other lineage (Fig. 3B). Consequently, the populations become trapped in one of the lineages, and unlikely to produce the crossover drug. For example, once the first innovation A1 is discovered and transferred to other individuals, drug triads including the new ingredient are on average superior to any of the other triads, and therefore B1 becomes less likely to be discovered; once A2 is discovered and transmitted to all other nodes, progress along the B trajectory becomes even less likely. In contrast, transmission across multilevel social structures of hunter-gatherers allows the coexistence of the two lineages among different kin or households clusters within camps, and among distinct camps in a multi-camp structure. The coexistence of cultural lineages promotes their faster recombination into higher-order cultural innovations (Fig. 3A). Thus, multilevel structuring favours the maintenance of cultural lineages and innovations in different parts of the network, due to a network memory of features that otherwise would be lost by single individuals.

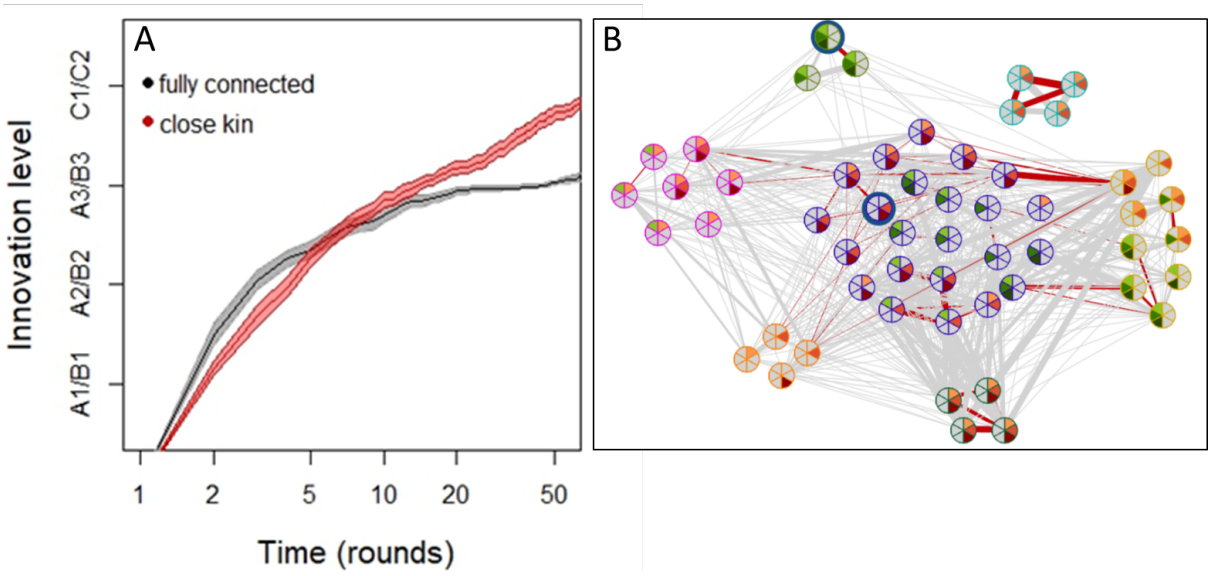

Fig. 4. Timing and diversity of innovations across real multi-camp social networks. A) Average innovation level (incremental steps A1, A2, A3, B1, B2, B3, and crossover event) by number of rounds, in fully connected (black) and real networks with transmission only to close kin (red). Averages were drawn from 1000 simulations for each transmission scenario. Shaded areas around the curves are standard errors estimated for each round and multiplied by 5 for better visualisation. B) Real multi-camp network (forest group) showing innovation level achieved by each individual at the end of one typical simulation with transmission only to close kin (light green: A1; green: A2; dark green: A3; light red: B1; red: B2; dark red: B3; the two blue circled individuals are the ones discovering the crossover). Innovations are clustered in different parts of the real network.

Finally, we asked how characteristics of hunter-gatherer sociality (high-mobility, strong kinship ties, non-kin dyads between households and camps) relate to the process of cultural accumulation. First, simulations show that as innovations become more complex from A1/B1 to crossovers, the contribution of non-kin dyads steadily increases from 49% to 55% (forest group), and from 59% to 65% (coastal group; Table S4). In addition, the contribution of inter-camp dyads also increases from 39% (A1) to 61% (crossover) in the forest group, and from 31% to 36% in the coastal group. Dyads formed by individuals from different camps (either kin or non-kin) often bridge together solutions from different parts of the network, which leads to the recombination of trajectories A and B into crossovers. This reveals the importance of high inter-camp mobility of individuals and families to cumulative culture in hunter-gatherer societies.

Unlike non-human primates, extant hunter-gatherers exhibit a social structure containing clusters of nuclear families that co-reside with other unrelated families, a fluid social structure including both male and female migrations, and friendship dyads across camps (*1-3*). We have provided evidence that multiple levels of clustering in hunter-gatherer social networks accelerate cumulative cultural evolution. This occurs because multilevel social structuring restricts transmission of cultural innovations and allows for the coexistence of multiple traditions or solutions to a similar problem in different parts of the network. The conclusion is consistent with differences in medicinal knowledge between BaYaka hunter-gatherers and African apes living in the same Central African forests (*11*). Of the 32 medicinal plants used by the BaYaka, 9 are used by gorillas and 6 by chimpanzees (*20*). However, no BaYaka individual in the sample had knowledge of all the 32 plants. This difference in knowledge breadth mirrors differences in social structure among the species, and suggests a redefinition of the 'ratchet effect' in humans: cumulative culture involves not only the impossibility of recreation of cultural features by isolated individuals, but also the emergence of knowledge specialisation within populations. Accordingly, in our simulations across real networks no individual ended up in possession of all innovations. This illustrates why cumulative culture is a product of human populations rather than individuals, and suggests that the origin of knowledge specialisation in the humans took place in hunter-gatherer multilevel societies.

We propose that the multilevel structure observed in extant hunter-gatherers may explain the cultural dynamism of *Homo sapiens* since its origins and its worldwide expansion. We believe that multilevel structuring already characterised Middle Stone Age populations emerging as early as 320,000 years ago, which were also known to have established trade dyads connecting sites up to 160 km apart (*7*, *21*). As hunter-gatherers expanded within and then out of Africa in small and interconnected bands, potential consequences may have included cultural recombination preceding 'local revolutions' such as the Upper Palaeolithic (*22*) and genetic introgression among *Homo sapiens* and other hominin species (*23*, *24*).

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Supplementary Materials for

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This PDF file includes:

Materials and Methods

Collection of network data using motes.

We have previous described the technology in detail (3), so here we provide a shorter description. Our device is a customised UCMote Mini with main processor, wireless communication module, memory storage unit and a four-week battery (software-optimised for low energy consumption), supporting the TinyOS operating system developed at the University of California, Berkeley.

Software.

We wrote the embedded C and nesC software to iteratively optimise parameters (frequency of beacons, strength of wireless communications, length of sleep phases). Each device sends beacons every 2 minutes, receiving beacons from other devices within a 3-meter range and storing them in long-term memory. Data were later downloaded via a PC side application written in JAVA. Radio links were adjusted to record other radio signals within 3 meters. Low power listening was used to reduce battery usage.

Motes utilisation.

Motes were waterproofed and sealed into wristbands. All participants signed an informed consent form and received a mote with ID number and coloured string. Individuals wore motes uninterruptedly for four weeks and received a small compensation (thermal bottle, cooking utensils). We checked for armband swaps and made adjustments before data processing.

Data recovery.

We ran raw data through a stringent data-processing system in Python to prevent data corruption. Data were matched to ID numbers and start-stop times of each mote. The result was a matrix with the number of recorded beacons for all possible dyads (or dyadic weights).

Ethical approval.

Research project and fieldwork were approved by the UCL Ethics Committee (code 3086/003, Leverhulme Trust grant RP2011-R-045, 2011-2016).

Description of cultural evolution model.

We performed agent-based simulations adapted from the model proposed by Derex and Boyd (10). The cultural repertoire of each individual is described by a binary vector (present/absent) where each entry represents a different ingredient or drug derived from a medicinal plant. Each ingredient has an intrinsic fitness or medicinal value. At time t=0 (start of simulation), an agent is endowed with a set of six original ingredients (two drugs of value 10, two of value 8, and two of value 6). Their recombination into triads may lead in some cases to the discovery of new ingredients of higher fitness, which are then added to the original set.

Starting with the six original ingredients, one triad (combining three drugs of medicinal values 10, 8 and 6) produces a first cultural innovation of higher medicinal value A1. All other triads were considered as non-successful and awarded no value. Next, another single triad including A1 plus the original ingredients produces a second drug A2 of even higher value; A2 is added to the drug set, and required for the creation of the higher-value drug A3. The same process generates a second trajectory B1, B2 and B3. The fitness of the new ingredients A1 and

B1 is greater than the fitness of any other triad; the same is true for A2/A3 and B2/B3. At the final stage of the experiment, two possible 'crossover' can be produced by the combination of ingredients from the trajectories A and B (crossover 1 requiring A3, B3 and A2; crossover 2 requiring A3, B3 and B2). Thus, cultural evolution from level 1 to 3 is vertical and defines two independent trajectories A and B, while cultural evolution from level 3 to 4 is horizontal and represents a rarer innovation leap. The values of the new ingredients were the same as in (*10*):

A1=B1=48
A2=B2=109
A3=B3=188
Crossover 1=Crossover 2=358

Simulations across fully connected networks.

Simulations of the model are based on dyad interactions between agents i and j. First we describe the case of a fully connected network of N individuals, i.e. a well-mixed population of N agents with equal probability of interaction to each other. The process of cultural evolution is simulated by a Monte Carlo method with asynchronous update. The simulation proceeds in epochs (or rounds):

1. a focal agent i is uniformly and randomly selected with probability p=1/N.
2. a second and neighbouring agent j is also randomly and uniformly selected. Since the network is fully connected, agent j is selected with a fixed probability p=1/(N-1).
3. i and j select respectively 2 and 1 objects from their set of ingredients (or vice-versa, with probability p=0.5), with probability proportional to their medicinal value, creating a drug triad.
4. if the combination leads to a discovery, the new drug is added to the set of ingredients of both discoverers i and j, otherwise nothing happens.
5. In case of discovery, all neighbours of i and j acquire the new discovery too. Since the network is fully connected, all nodes or agents are connected, and the whole population acquires the new ingredient immediately following its discovery.

When all N individuals have been selected as focal agents in step 1, an epoch t ends. When a crossover is discovered at time t=T, the simulation ends.

Simulations across real hunter-gatherer networks.

We simulated the model across the real weighted networks of Agta hunter-gatherers (derived both from two multi-camp groups and from six individual camps). This was possible thanks to the modification of a few of the steps above. To simulate the process with transmission of discoveries to all neighbours, new steps 2 and 5 are defined as:

2. a second agent j, neighbour of i, is selected. For each neighbour j, selection probability is proportional to the weight of the dyadic link wij between i and j.
5. In case of discovery, only neighbours of i and neighbours j acquire the new ingredient.

To simulate transmission of discoveries only to close kin across the real network, step 5 was further modified:

5. In case of discovery, only neighbours of i who are also close kin of i, and neighbours of j who are also close kin of j acquire the new ingredient.

		Close kin	Extended kin	Non-kin
Unweighted dyads				
Forest	**intra**	36 (16.5%)	27 (12.3%)	156 (71.2%)
	inter	14 (3.7%)	57 (15.3%)	303 (81%)
	total	50 (8.4%)	84 (14.2%)	459 (77.4%)
Coast	**intra**	20 (6.8%)	32 (10.9%)	242 (82.3%)
	inter	18 (6.2%)	34 (11.8%)	237 (82%)
	total	38 (6.5%)	66 (11.3%)	479 (82.2%)
Weighted dyads				
Forest	**intra**	4072 (39.3%)	1924 (18.6%)	4358 (43.1%)
	inter	737 (6.9%)	2771 (25.9%)	7186 (67.2%)
	total	4809 (22.9%)	4695 (22.3%)	11544 (54.8)
Coast	**intra**	1618 (6.9%)	2919 (12.4%)	18946 (80.7%)
	inter	444 (5.3%)	836 (9.9%)	7138 (84.8%)
	total	2062 (6.4%)	3755 (11.8%)	26084 (81.8%)

Table S1. Distribution of intra-camp, inter-camp and total dyads by kinship level in forest and coastal multi-camp groups. When dyadic weights are considered, the proportion of close kin dyads is significantly higher at intra- than inter-camp level both in the forest (χ^2=26.5; P<10^{-6}) and coastal (χ^2=3138; P<10^{-14}) groups.

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			M-M	F-F	M-F	Test statistics
Unweighted dyads						
Forest	Intra	observed	35	72	112	χ^2=2.17; P=0.34
		predicted	69	98	164	
	Inter	observed	76	116	182	χ^2=1.25; P=0.54
		predicted	231	308	561	
	Total	observed	111	188	294	χ^2=2.72; P=0.26
		predicted	300	406	725	
Coast	intra	observed	85	56	153	χ^2=0.03; P=0.99
		predicted	90	57	159	
	inter	observed	78	70	141	χ^2=0.47; P=0.79
		predicted	100	79	181	
	total	observed	163	126	294	χ^2=0.27; P=0.87
		predicted	190	136	340	
Weighted dyads						
Forest	intra	observed	3179	1902	5613	χ^2=491.2; P<10^{-10}
		predicted	2229	3166	5299	
	inter	observed	1675	2592	6087	χ^2=182.2; P<10^{-10}
		predicted	2159	3066	5130	
	total	observed	4854	4494	11700	χ^2=378.1, P<10^{-10}
		predicted	4388	6232	10429	
Coast	intra	observed	5370	5238	12875	χ^2=243; P<10^{-10}
		predicted	6789	4473	12221	
	inter	observed	2150	1690	4578	χ^2=61.6; P<10^{-10}
		predicted	2272	2039	4107	
	total	observed	7520	6928	17453	χ^2=174.8, P<10^{-10}
		predicted	8919	6895	16087	

Table S2. Distribution of intra-, inter- and total dyads by sex composition in forest and coastal multi-camp groups. M-M: male-male; F-F: female-female; M-F: male-female. In the case of unweighted dyads, the predicted inter-, intra-, and total distribution was calculated as the expected proportions under the assumption of random inter- and intra-camp association between all males and females in each group (forest and coastal), and for this reason the total number of predicted dyads is larger than the observed number. The predicted distribution of weighted dyads is an extrapolation of the proportions of the observed sex distribution of unweighted dyads. For this reason, the total number of predicted and observed dyads is the same. Test statistics were derived from chi-square tests comparing observed and predicted distributions.

	Time to crossover (t)				
Camp size	Fully connected, all neighbours		Real network, all neighbours		Real network, close kin only
18	1545.4	95% CI: [-7, 151]; P=0.07	1460.1	**95% CI: [600, 727]; $P<10^{-15}$**	680.8
26	1035.2	95% CI: [-43, 63]; P=0.71	1026.2	**95% CI: [428, 518]; $P<10^{-15}$**	475.7
33	835.4	**95% CI: [129, 211]; $P<10^{-10}$**	640.4	**95% CI: [273, 336]; $P<10^{-15}$**	233.5
36	746.6	95% CI: [-28, 49]; P=0.61	727.5	**95% CI: [420, 488]; $P<10^{-15}$**	169
39	650.5	95% CI: [-46, 23]; P=0.53	659.4	**95% CI: [388, 446]; $P<10^{-15}$**	142.5
48	558	**95% CI: [33, 89]; $P<10^{-4}$**	503.3	**95% CI: [246, 295]; $P<10^{-15}$**	128.8
Multi-camp group					
37 (coast)	697.8	**95% CI: [13, 81]; P=0.006**	646.7	**95% CI: [367, 424]; $P<10^{-15}$**	119.9
54 (forest)	477.3	**95% CI: [180, 222]; $P<10^{-15}$**	230.6	**95% CI: [56, 73]; $P<10^{-15}$**	51.2

Table S3. Time to crossover as a function of camp size, network type and transmission mode. Each time to crossover (t) is the mean value of 1000 simulations. Fully connected networks, all neighbours: innovations transmitted to all neighbours (i.e. all nodes). Real network, all neighbours: innovations transmitted only to nodes directly linked to innovating dyad, with network topology as in the real Agta camps or multi-camp groups. Real network, close kin only: innovations transmitted only to close kin individuals directly linked to innovating dyad, with network topologies also as in real Agta groups. The two columns with tests statistics represent the results of Wilcoxon rank tests between the adjacent columns. Significant tests ($P<0.05$) shown in bold. Also shown are the 95% confidence interval of the difference between group means.

Camp	Innovation Level	Close kin	Extended kin	Non-kin	Intra-camp	Inter-camp
Forest	A1/B1	0.314	0.192	0.494	0.608	0.392
	A2/B2	0.297	0.206	0.497	0.571	0.429
	A3/B3	0.276	0.219	0.505	0.524	0.476
	Crossover 1/2	0.205	0.246	0.550	0.385	0.615
Coast	A1/B1	0.240	0.169	0.591	0.690	0.310
	A2/B2	0.224	0.178	0.600	0.692	0.308
	A3/B3	0.197	0.183	0.620	0.682	0.318
	Crossover 1/2	0.144	0.201	0.655	0.642	0.358

Table S4. Fraction of dyads classified by relatedness (close kin, extended kin, non-kin) or location (intra-camp, inter-camp) and estimated at successive innovation level (A1/B1, A2/B2, A3/B3, Crossover 1/2). Data are from simulations (n=1000) based on real hunter-gatherer network, and transmission of innovations to close kin only.

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